into contact with the shell or any other region of the burrow."

Yonge (1955) made observations on Lithophaga plumula (Hanley, 1844) at Pacific Grove, California. He actually saw a specimen of Lithophaga extrude its anterior mantle tissue and place it in intimate contact with the rock at the head of a broken burrow. Yonge was unable to detect any free acid on the surface of the fused inner lobes of the mantle. He did confirm the glandular areas, both anterior and posterior, that were described by Carazzi, List, and Pelseneer. Yonge postulated an acid mucous secretion from these glands. The anterior gland would do the original softening and the posterior gland would widen the burrow as the animal grows in size. Yonge saw cilia on the protruded anterior mantle tissue and suggested that these cilia carry the dissolved rock and mucus ventrally and then posteriorly into the mantle cavity. This dissolved material then passes posteriorly and out the dorsal surface of the inhalant siphon, which is the usual tract for the removal of pseudofeces.

Three authors, Berry (1907), Amemiya (1933), and Haas (1942), have reported finding Lithophaga plumula in non-calcareous substrates. Berry claims to have found L. plumula in hard blue clay dredged from 12 fathoms in Monterey Bay. The Lithophaga were found with other pelecypods which are known to bore mechanically, such as Botula, Parapholas californica (Conrad, 1837), and three species of Pholadidae. Amemiya (1933) reported finding Lithophaga in tuffaceous mudstone. He did not test the mudstone for calcium carbonate content. Haas (1942) collected L. plumula in lime-cemented sandstone and in non-calcareous argillaceous shale, both at La Jolla and at Pacific Grove, California. The first two authors mentioned did not comment on the methods of boring. Haas (1942) offered no theories on chemical or mechanical boring except to state that the boring could not be chemical. The reason he gave for this statement was that he had found Lithophaga in non-calcareous shale along with Irus lamellifer (Conrad, 1837), Botula californiensis Philippi, 1847, and some pholads. If this be true, it would suggest that Lithophaga can bore mechanically.

MATERIALS AND METHODS

Field and laboratory studies were made at the Kerckhoff Marine Laboratory, Corona Del Mar, California. Further laboratory experiments were conducted at the University of California, Berkeley, California. The specimens used for these studies were collected at Carpenteria, California, and at Corona Del Mar. The specimens were identified by Dr. L. G. Hertlein of the California Academy of Sciences as Lithophaga plumula kelseyi Hertlein and Strong, 1946. This subspecies is found from San Diego, California, to Duxbury Reef, immediately north of San Francisco Bay and is shown in Plate 25, figures 1, 2, 3, and 4.

Two separate experiments were set up for the observation of Lithophaga in the laboratory in both artificial and natural burrows. In the first experiment, which will be identified as Experiment No. 1, ten of the mussels were left on the bottom of a five-gallon tank of aerated sea water. No burrows were provided. Three others were put into Pyrex test tubes of approximately the same diameter as the original burrows, and five were put into holes bored in limestone rock with a tungsten-carbide drill bit. The shape of the bottom of the holes in the limestone is shown by the dotted line across the bottom of the hole in textfigure 1. The purpose of this experiment was to observe the animals and to determine if they could live for a protracted period in the laboratory.

The second experiment (No. 2) was a controlled experiment in which freshly collected specimens of Lithophaga plumula kelseyi were placed in holes bored in the same limestone as that used in Experiment No. 1, and in a non-calcareous mudstone. The limestone had a

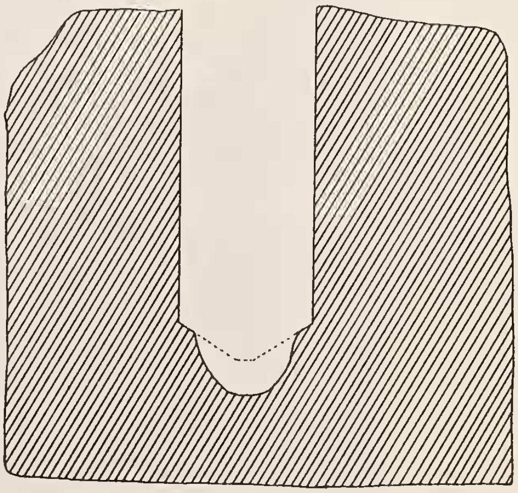

Figure 1: Cross section of a typical artificial burrow in limestone and mudstone showing extent of boring activity by *Lithophaga*

hardness equal to fluorite (number 4 on the hardness scale). The mudstone had a hardness of 3, equivalent to calcite. The mudstone was obtained from Duxbury Reef, Bolinas, California, and is a rock in which numerous mechanically boring mollusks such as Botula, Platyodon, and Pholadidea are found. Lithophaga were placed in the holes in the two pieces of rock, and the rocks were put into a five-gallon aquarium filled with sea water which was kept aerated at all times. Experiment No. 1 lasted one year, followed by Experiment No. 2 which was continued for six months.

The purpose of Experiment No. 2 was to compare the boring abilities of Lithophaga in a rock which can be attacked and dissolved by chemical action, namely, calcium carbonate or limestone; and in a rock that cannot be affected by an acid or by chemical activity, viz., non-calcareous mudstone. Additional observations were made on the rotation of the animals in the mudstone and limestone burrows.

Miscellaneous observations were made on animals from both of the above-mentioned experiments in regard to deposits on the burrow walls. The anterior end of one of the natural burrows was broken off, and the activities of the anterior mantle tissue of the enclosed specimen was observed.

OBSERVATIONS AND RESULTS

Lithophaga Burrows in Nature

In nature Lithophaga burrows are found in carbonate-cemented sandstone and calcareous shale. The inside of the burrow is a little longer than the animal, which allows it to move back and forth by the action of the byssal retractor muscles. When the animal is in its extreme posterior position, the ends of the "plume" are level with the plane of the entrance of the burrow (textfig. 2). The aperture is small and is usually found with a mass of white limy material surrounding it and extending it above the rock surface for a distance of about two millimeters. This white material fizzed and produced CO_2 gas when it was treated with dilute hydrochloric acid. The cation was not determined but was presumed to be calcium.

The sandstone burrows were variably lined with a white substance which also proved to be a carbonate and was thus assumed to be calcium carbonate. In all cases the posterior third was lined and in some cases observed the entire burrow was lined, as in Plate 25, figure 5.

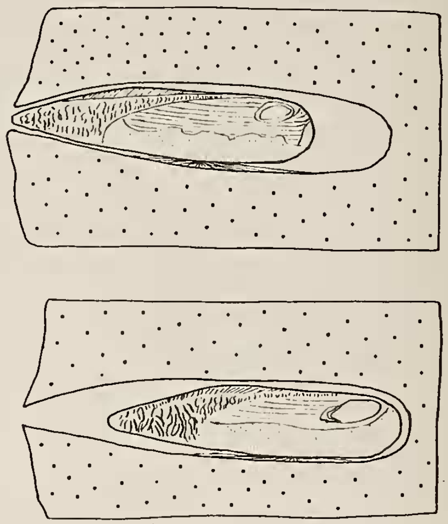

Figure 2: *Lithophaga* in its most posterior position (top) and most anterior position (bottom) in its natural rock burrow.

Experimental Results

The main purpose of Experiment No. 1 was to determine the length of time Lithophaga could live under laboratory conditions in a five-gallon tank of sea water both inside and outside the confining burrows. The specimens in the artificially bored limestone burrows, in the test tubes, and on the bottom of the tank all lived through a period of one year. No attempt was made to feed the animals, and the water was not changed. It was noted, however, that there was a fairly uniform algal growth on the rocks and on the walls of the tank, indicating that free-

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Explanation of Plate 25

Figures 1 to 4: *Lithophaga plumula kelseyi.*

Figure 1: Ventral view. Figure 2: Dorsal view. Figure 3: Lateral view. Figure 4: Lateral view.

Figure 5: A longitudinal section of a *Lithophaga* burrow in lime-cemented sandstone showing complete calcareous lining.

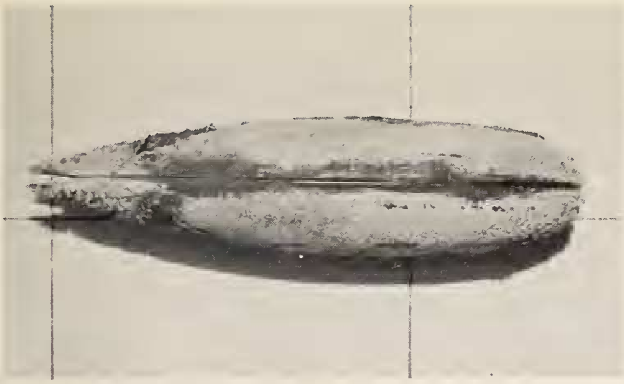

Figure 1

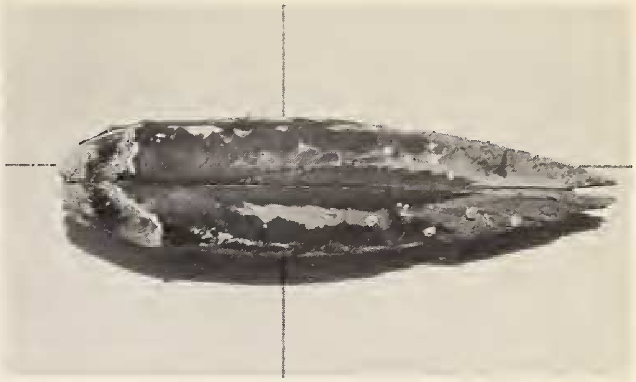

Figure 2

Figure 3

Figure 4

Figure 5

HODGKIN, *photo.*

Bottom of the burrow of Textfigure 3. The dark area in the center is the erosion caused by the specimen of *Lithophaga* that was unable to rotate. Notice the symmetry across the dorso-ventral axis.

HODGKIN, *photo.*

swimming algal gametes were probably available for food.

The three groups of Lithophaga all deposited a material assumed to be calcium carbonate. The specimens on the bottom of the tank placed their deposits flat on the glass bottom adjacent to their ventral surface where they had attached themselves by their byssal threads.

The observation that led directly to Experiment No. 2 was that the specimens of Lithophaga left in the limestone holes all continued to bore into the rock. After the animals were removed, symmetrical, concave depressions were seen at the bottom of the holes as shown in textfigure 1. The volume of material removed by the two largest Lithophaga (about 6 cm. in length) was measured and found to be 0.12 cm^3 in one case and 0.17 cm^3 in the other case.

The next point to determine was whether Lithophaga could elongate artificially-bored holes in a non-calcareous mudstone under laboratory conditions similar to those in Experiment No. 1. Experiment No. 2 was set up with a block of mudstone from Duxbury Reef, and a new piece of the same limestone that was used in Experiment No. 1 was used as a control.

The result of Experiment No. 2 was that all four specimens of Lithophaga continued to bore into the limestone but none of the three individuals in the mudstone had any effect whatsoever on that rock. No erosion could be detected, even microscopically, on the bottom of the mudstone holes. The bottoms of the holes in the mudstone remained as they had been bored by the drill, as shown by the dotted line in textfigure 1. The volume of material removed from the limestone by three of the Lithophaga was measured and found to be 0.18, 0.23, and 0.12 cubic centimeters, respectively. The fourth Lithophaga burrow was not measured because of accidental fracture of the rock. This particular specimen was slightly larger than the others and as a result was not able to rotate in its burrow as did the others. The shape of the excavation caused by this particular animal is significant as proof against a mechanical theory of boring and is discussed at the end of this section and in the conclusion.

Rotation of the Lithophaga specimens in their burrows was observed during Experiment No. 2 and checked by the actual byssal attachments at the conclusion of the experiment. Both groups rotated very little, but it was noted at the end of the experiment that the animals in the mudstone as a group rotated less than those in the limestone. In natural burrows the points of attachment around the inside are quite regular, indicating that the animal in nature does not seem to favor any one position.

One of the Lithophaga in the limestone of Experiment No. 2 was too large to rotate freely. It was able to gape a very slight amount, however, and this gape was sufficient to allow anterior mantle tissue to flow out and up against the head end of the artificial burrow. The excavation was symmetrical about the projection of the dorso-ventral axis on the head end of the burrow, but it was not radially symmetrical. The holes eroded by the Lithophaga which were free to rotate in both Experiments 1 and 2 were very nearly radially symmetrical. Textfigure 3 and Plate 26 show the shape of the hole eroded by the individual which was stuck in its hole. Records of the rotation of all the animals were kept throughout the experiment. At no time was the specimen which made the boring shown in textfigure 3 and Plate 26 seen to rotate. As further evidence against rotation by this animal the points of byssal attachment were checked after the animal was removed. Only one small area was covered heavily by the byssus implantations, proving that the animal kept its dorso-ventral orientation constant during the experiment.

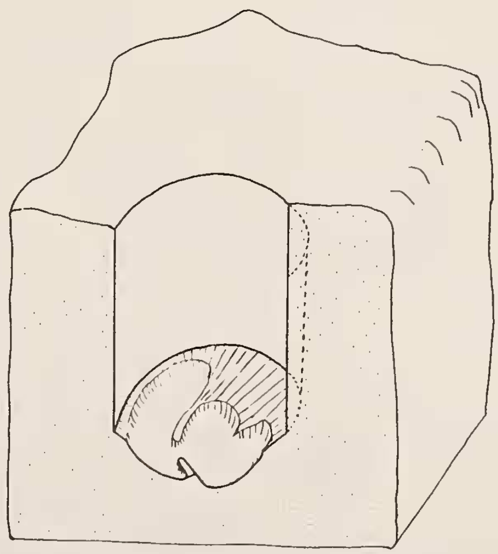

Figure 3: View of artificial burrow in limestone in which the animal was unable to rotate. The plane of the break in the rock is almost in the plane of symmetry of excavation.